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Impact of *Dreissena* fouling on the physiological condition of native and invasive bivalves: interspecific and temporal variations

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Abstract The impact of *Dreissena* fouling on unionids has hardly been studied in Europe, despite the fact that in some ecosystems (e.g. Lake Balaton, Hungary) infestations of several hundreds to a thousand individuals per unionid have been observed. At present, the zebra mussel *Dreissena polymorpha* is a dominant species in Lake Balaton and in the last decade three other invasive bivalves were introduced, potentially increasing the pressure on native unionid survival. We examined whether the fouling of dreissenids (zebra and quagga (*D. rostriformis bugensis*) mussels) has a negative impact on native (*Anodonta anatina*, *Unio pictorum* and *U. tumidus*) and invasive (*Corbicula fluminea* and *Sinanodonta woodiana*) bivalves and whether there are any interspecific and temporal variations in fouling intensity and physiological condition measured by standard condition index and glycogen content. A significant negative impact was detected on native unionids only in July and September (no impact was detected in May), when the fouling rate was high. For invasive species, a significant negative impact was detected on *S. woodiana* with a high level of dressenid infestation; whereas no significant impact was detected on *C. fluminea*. Overall, this study confirms that *Dreissena* may threaten unionid species including the invasive *S. woodiana*, although high interspecific and temporal variations were observed. This situation should be taken into account in future ecological and conservational assessments because species respond differently to *Dreissena* fouling and effects seem to be more pronounced in late summer/early autumn. In addition, this study provides the first evidence that the invasive *C. fluminea* appear to be less vulnerable to dressenid fouling.

Keywords Native unionids · *Dreissena* infestation · *Corbicula fluminea* · *Sinanodonta woodiana* · Lake Balaton

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Introduction

Over recent decades, the introduction and spread of non-indigenous species in European fresh waters has accelerated greatly due to the increasing number of interconnected waterways, the globalization of

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international trade and the extended use of recreational vessels (Aldridge et al. 2004; Bij de Vaate et al. 2002; Galil et al. 2007; Bódis et al. 2012; Jackson and Grey 2012). In freshwater ecosystems bivalves represent one of the faunal groups with high levels of introduction. Some bivalve species can be considered highly invasive and in some circumstances they became dominant in terms of density and biomass in benthic communities and also bring new attributes to the invaded ecosystem (Balogh et al. 2008; Sousa et al. 2008a, 2008b; Werner and Rothhaupt 2008; Aldridge 2010; Karatayev et al. 2010). In addition, they can make a significant ecological impact by altering the structure and function of invaded ecosystems (Strayer et al. 1999, 2004; Strayer and Smith 2001; Sousa et al. 2009, 2011b, in press; Strayer 2010; Ilarri et al. 2012), and in some cases these pests may cause high economic losses due, for example, to biofouling (for a review see Mackie and Claudi 2010).

One of the most important (and most widely studied) invasive species in freshwater ecosystems is the zebra mussel *Dreissena polymorpha*, which is listed among the 100 worst invasive species (Lowe et al. 2000), triggering severe direct and indirect ecological and economic consequences worldwide (Karatayev et al. 1997; Strayer et al. 1999; Connelly et al. 2007; Keller et al. 2007; Strayer 2009, 2010; Mackie and Claudi 2010; Sousa et al. 2011a, in press). One of the most remarkable effects involves the fouling of unionids. Indeed, the posterior end of the unionid shells exposed to the water column can be colonized by *D. polymorpha*, which affects filtration rates, hinders locomotion and burrowing behaviour, and causes valve occlusion and suffocation of the unionids (Schloesser et al. 1996). All these effects may reduce energy storage, growth rates, fecundity and in severe cases may lead to mortality (Sousa et al. 2011a).

The impact of *D. polymorpha* on unionids in North America has been extensively studied since its introduction in the 1980s (Haag et al. 1993; Nalepa 1994; Schloesser and Nalepa 1994; Ricciardi et al. 1995, 1996, 1998; Ricciardi 2003; Schloesser et al. 1996; Strayer and Smith 1996; Strayer and Malcom 2007). However, in Europe less attention has been paid to this important conservation issue (Karatayev et al. 1997; Burlakova et al. 2000; Sousa et al. 2011a), despite the fact that in some ecosystems (e.g. Lake Balaton, Hungary) infestations of several hundreds to a thousand *D. polymorpha* per unionid have been observed after its establishment (Sebestyén 1937; Lewandowski 1976).

At present, bivalves from the family Unionidae are considered to be one of the most endangered groups of animals on the planet, since their diversity has declined both locally and globally (Bogan 1993; Lydeard et al. 2004). Therefore, studies addressing possible effects that impair unionid survival should be a conservational priority in order to mitigate, for example, the negative effects caused by the introduction of invasive species. Special attention should be also paid to studies addressing interspecific and temporal variations in the overall effects.

Lake Balaton, the largest lake in Central Europe, had been an isolated water body until the opening of the Sió Canal, which created conditions for the spread of invasive species from the River Danube. In the last decades one of the most important ecological changes in the lake has involved the successful establishment of Ponto-Caspian species (e.g. *D. polymorpha* and *Chelicorophium curvispinum*) (Muskó et al. 2007; Balogh et al. 2008). The zebra mussel, *D. polymorpha*, appeared and spread throughout Lake Balaton in the 1930s (Sebestyén 1934, 1937), and it has remained dominant since its introduction. In comparison with other European and North American lakes, the density of *D. polymorpha* can reach very high levels (220,000 ind. m^{-2}, Balogh et al. 2008). The number of successful introductions of invasive species in Lake Balaton has increased since the 1930s, leading to further changes in ecosystem functions and services (Bíró 1997; Muskó et al. 2007; Majoros 2009). Over the last decade, three other invasive bivalves were introduced, potentially increasing the pressure on native unionid survival. The Chinese pond mussel *Sinanodonta woodiana* (Lea 1834) was first described in Lake Balaton in 2006, and its mean density recently attained 1–2 ind. m^{-2} at sites with mud substrates (Benko-Kiss et al. 2012). Although this density may be considered very low compared with other invasive bivalves, we cannot forget that this species may reach a very high biomass due to its large size. Moreover, recent studies described massive die-offs during drought conditions with potentially serious ecological effects in the Danube River basin (Bódis et al. in press). In addition, the quagga mussel *Dreissena rostriformis bugensis* and the Asian clam *Corbicula fluminea* were also introduced into the lake in 2008

(Majoros 2009), and a rapid spread of *D. rostriformis bugensis* was recorded, reaching a maximum density of 9,061 ind. m^{-2} on hard substrates by 2011 (Balogh and Purgel 2012).

Given the lack of studies addressing the potential impact of dressenid infestation on other bivalves in Europe, and since this situation may constitute an important conservation issue, the main aims of this study were: (1) to examine whether the fouling of dreissenids may affect the physiological condition of other bivalve species, including native (*Anodonta anatina*, *Unio pictorum* and *Unio tumidus*) and invasive (*S. woodiana* and *C. fluminea*) bivalves; (2) to assess possible interspecific and temporal patterns in fouling intensity and impact on physiological condition measured by glycogen content and standard condition index; and (3) to assess the possible contribution of the surface area of the bivalves exposed to the water column when explaining interspecific and temporal variations in the fouling rates.

Methods

Study area and sampling strategy

The study area was Lake Balaton, the largest shallow lake in Central Europe (mean depth: 3.25 m; greatest depth: 10.2 m; length: 78 km; average width: 7.6 km and surface area: 596 km^2). The sampling was carried out at Keszthely (46°44′43.41″N, 17°14′50.94″E) located in the south-western region of the lake. The Keszthely basin is the most eutrophic region of Lake Balaton because nutrients mainly enter the lake in this area via the River Zala (Herodek 1984). In addition, *C. fluminea* with different *Dreissena* fouling rates were collected at Balatonfenyves, located on the southern side of the lake (46°42′56.66″N, 17°28′46.03″E) because a high number of infested specimens could only be found at this site. The bottom substrate contains mainly mud and silt at Keszthely but consists of silt and sand at Balatonfenyves. To assess the current conservational status of native unionids and the proliferation of invasive bivalves (*C. fluminea* and *S. woodiana*) at our study sites, we measured their density using 20 randomly placed quadrats (area of each quadrat 0.25 m^2) in the littoral zone at a water depth of 1 m in July. Searches in each quadrat were carried out until no more bivalves were found to a sediment depth of 20 cm.

For the physiological status assessment, three native (*Anodonta anatina*, *Unio pictorum* and *Unio tumidus*) and two invasive (*Sinanodonta woodiana* and *Corbicula fluminea*) bivalve species with different fouling intensities of dreissenids were collected by hand in May, July and September 2012. The sample sizes were as follows: 105 *S. woodiana* (31 in May, 38 in July and 36 in September), 39 *A. anatina* (8 in May, 8 in July and 23 in September), 98 *U. pictorum* (33 in May, 35 in July and 30 in September), 109 *U. tumidus* (44 in May, 35 in July and 30 in September) and 33 *C. fluminea* in July. The collected unionid individuals were split into four groups according to their infestation intensity: uninfested (without dreissenids); lightly infested (0–1 g wet mass of dreissenids attached, 1–5 specimens); moderately infested (1–10 g wet mass of dreissenids attached, 5–50 specimens); and heavily infested (>10 g wet mass of dreissenids attached, >50 specimens). In view of the considerable differences in body size and infestation intensity, for *C. fluminea* we used a different infestation classification: uninfested (without dreissenids); lightly infested (0–0.6 g wet mass of dreissenids attached, 1–3 specimens); moderately infested (0.6–2 g wet mass of dreissenids attached, 3–10 specimens); and heavily infested (>2 g wet mass of dreissenids attached, >10 specimens).

Immediately after collection, the bivalves were transported to the laboratory in aerated water. The maximum length of each unionid and the wet mass after blotting dry were measured. For each infested bivalve, the number and the wet mass of attached dreissenids were recorded. In addition, the species of dreissenids were identified and their shell length was measured. For each unionid the surface area of shell exposed in the water column was estimated by covering the exposed part of the shell (denoted by the presence of algae and calcareous deposits) with aluminium foil, which was subsequently weighed and converted to area using a standard area-mass ratio (following Ricciardi et al. 1995). Bivalves were stored in a freezer at −20 °C until required for the physiological analysis. To measure the physiological condition of each bivalve species, the standard condition index [dry tissue mass (g)/dry shell mass (g)] and the glycogen content were determined. The fact that glycogen content is independent of bivalve size makes

it a powerful tool for measuring the physiological condition (Sousa et al. 2011a). The whole soft body tissue was removed and dried to constant mass at 60 °C in an oven. Glycogen was measured colorimetrically using the phenol–sulphuric acid method following Baker and Hornbach (2000).

Data analysis

General linear models were performed to identify which factors and covariates have a significant impact on the fouling intensity and physiological condition using: (1) fouling intensity (measured by wet mass of attached dreissenids) as a dependent variable, and species, months, exposed area and shell length as independent variables; and (2) physiological condition (standard condition index and glycogen content) as a dependent variable and wet mass of attached dreissenids, species, months, exposed area and shell length as independent variables. The most appropriate model was chosen by using the Akaike's information criterion (AIC). Adjustment of the models was achieved by diagnostic plots, checking for linearity, normality, heteroscedasticity and influential observations. The exposed area and shell length were log transformed and the wet mass of attached dreissenids was square root transformed for variance homogenization.

Analysis of Variance (ANOVA) was carried out to test the differences in fouling intensity and exposed area between species and months of sampling and in physiological condition (standard condition index and glycogen content) between species, months of sampling and classes of infestation. Linear regression analysis was used to determine whether the exposed area per species has a significant impact on the fouling intensity (measured by wet mass of attached dreissenids) per month and whether the wet mass of attached dreissenids has a significant impact on the physiological condition (standard condition index and glycogen content) of the studied bivalve species per month. Pearson's correlation coefficients were calculated to determine the relationship between the exposed area of the bivalve species studied and the fouling intensity (measured by wet mass of attached dreissenids) and the physiological condition (standard condition index and glycogen content) of the bivalve species studied and the wet mass of attached dreissenids for each month. All statistical analyses were carried out by using R version 2.6.2 (R Development Core Team 2007).

Results

All the recorded bivalve species inhabiting Lake Balaton provided an appropriate substratum for the establishment of dreissenids (Fig. 1). Although *Anodonta cygnea* and *Pseudanodonta complanata* inhabit Lake Balaton, these species were not found at our study site (Keszthely) and the recorded mean density (±SD) of *A. anatina* was very low (1.6 ± 2.0 ind. m^{-2}). In contrast, the density of *U. pictorum* and *U. tumidus* was high (14.0 ± 5.3 and 14.4 ± 4.4 ind. m^{-2}). Regarding the invasive species, a high mean density (±SD) of *S. woodiana* was detected (6.0 ± 3.3 ind. m^{-2}) at Keszthely. The mean density of *C. fluminea* at Keszthely was 3.2 ± 3.1 ind. m^{-2}, whereas it reached more than 30 times higher values at Balatonfenyves (104.8 ± 29.3 ind. m^{-2}).

The following series of conclusions can be drawn based on general linear models: (1) the month of sampling, the exposed area and the shell length of the studied bivalves had a significant impact on the fouling intensity measured by the wet mass of dreissenids (adjusted $R^2 = 0.42$, $F = 10.25$, $p < 0.001$); (2) the wet mass of dreissenids, the species, and the month of sampling had a significant impact on the glycogen content (adjusted $R^2 = 0.62$, $F = 32.10$, $p < 0.001$); and (3) the wet mass of dreissenids, the species, the month of sampling, and the exposed area had a significant impact on the standard condition index (adjusted $R^2 = 0.74$, $F = 10.53$, $p < 0.001$).

Without taking into account *C. fluminea*, the mean fouling rates (measured by mean wet mass of dreissenids) showed no differences between species (ANOVA, $F = 0.33$, $p = 0.80$), although the mean fouling rates were significantly different between months of sampling (ANOVA, $F = 33.31$, $p < 0.001$) (Fig. 2). The fouling rates of all the unionids increased from May to September, reaching the highest fouling intensity in September, with the following maximum number and wet mass of dreissenids: *A. anatina* (152 specimens, 23.70 g wet mass), *S. woodiana* (171 specimens, 24.28 g wet mass), *U. tumidus* (112 specimens, 16.21 g wet mass), *U. pictorum* (111 specimens, 14.72 g wet mass). A maximum of 24 specimens and 3.56 g wet mass was observed on *C. fluminea*.

Dreissena rostriformis bugensis was also found infesting other bivalve species, but always at a low density. The mean shell size of *D. rostriformis bugensis* was significantly higher than *D. polymorpha*

Fig. 1 Photos showing *Dreissena* fouling on the bivalve species studied: *Anodonta anatina* (**a**), *Sinanodonta woodiana* (**b**), *Unio pictorum* (**c**), *Unio tumidus* (**d**), and *Corbicula fluminea* (**e**)

(ANOVA, $F = 136.71$, $p < 0.001$) and only large individuals (>5 mm) were recorded (Fig. 3). Newly settled juveniles of *D. polymorpha* were observed in July (<5 mm). The maximum length was 31.25 mm in zebra mussels and 28.05 mm in quagga mussels.

Without taking into account *C. fluminea*, the exposed area did not vary depending upon the month (ANOVA, $F = 0.54$, $p = 0.58$), but was significantly different between species. *Anodonta anatina* and *S. woodiana* had larger exposed surface area than *U. pictorum* and *U. tumidus* (ANOVA, $F = 234.4$, $p < 0.001$). Positive correlations were detected between the exposed area and the fouling intensity in all the bivalve species studied (Pearson's correlation, *A. anatina*: $r = 0.228$, *S. woodiana*: $r = 0.155$, *U. pictorum*: $r = 0.220$, *U. tumidus*: $r = 0.316$) but a statistically significant impact of the exposed area on the fouling intensity (measured by the wet mass of dreissenids) was found only in July in *S. woodiana* and *U. tumidus* (Linear Regression, $R^2 = 0.11$, $p < 0.05$ and $R^2 = 0.15$, $p < 0.05$, respectively) and in September in *S. woodiana*, *U. pictorum* and *U. tumidus* (Linear Regression, $R^2 = 0.25$, $p < 0.01$; $R^2 = 0.18$, $p < 0.05$ and $R^2 = 0.35$, $p < 0.001$, respectively, data not shown).

Based on the glycogen content, significant differences were detected between the uninfested bivalve

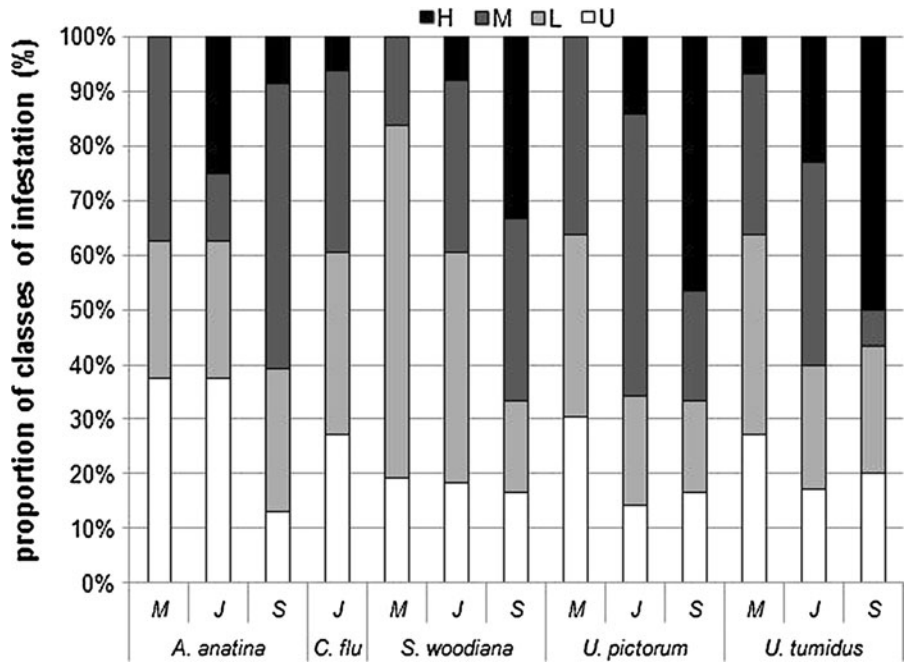

Fig. 2 Proportion of classes of infestation: uninfested (U), lightly infested (L), moderately infested (M), and heavily infested (H) according to species and months: May (M), July (J), and September (S)

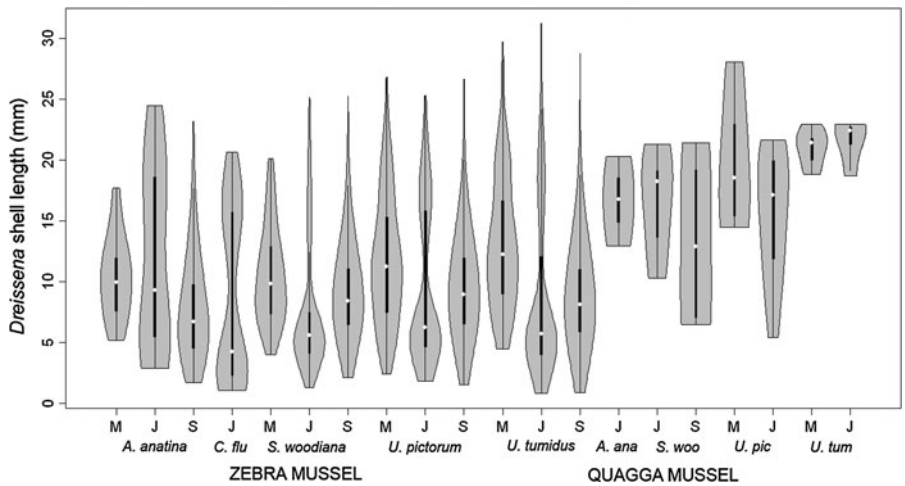

Fig. 3 Shell length frequency of attached zebra and quagga mussels on the bivalve species studied collected in different months: May (M), July (J) and September (S). The *violin plot* is a combination of a symmetrized kernel density plot and a *boxplot*. The *shape* of the *violin plot* (in *grey*) represents the density estimated by the kernel method. The *wider* the *shape* for a given shell length, the more specimens are associated with that value. The *white dot* represents the median value, the *thick line* segment illustrates the inter-quartile range between the first and the third ones, and the *thin line* represents the range of data without outliers

species (ANOVA, $F = 7.90$, $p < 0.001$) and between months per uninfested species (ANOVA, *A.anatina*: $F = 270.8$, $p < 0.001$; *S. woodiana*: $F = 9.42$, $p < 0.01$; *U. pictorum*: $F = 6.68$, $p < 0.01$; *U. tumidus*: $F = 4.10$, $p < 0.05$) (Fig. 4). Regarding all the months, the invasive *S. woodiana* had the highest mean glycogen content (38.8 %). The mean glycogen content of native species was similar but *A. anatina* showed the lowest value with 30.1 % (*U. pictorum* with 31.6 % and *U. tumidus* with 33.9 %). The glycogen content of *S. woodiana* was higher in May, decreasing in July and further decreasing in

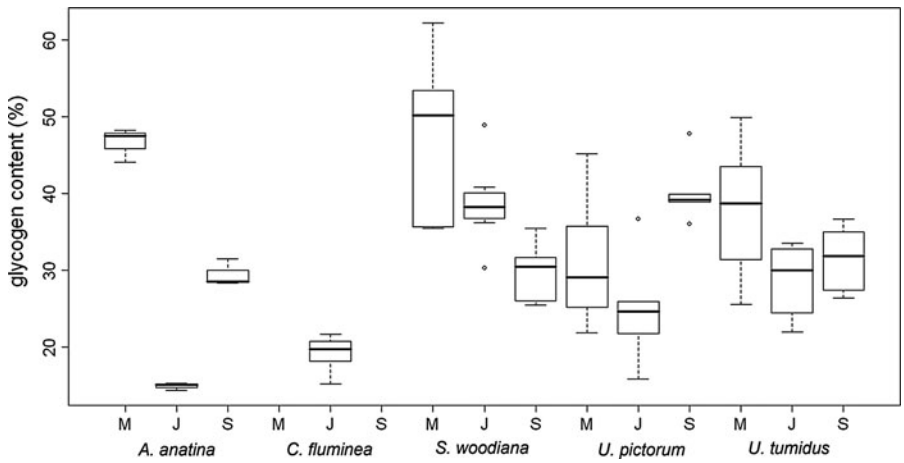

Fig. 4 Glycogen content of uninfested bivalve species according to months: May (M), July (J), and September (S)

September. The glycogen content of *A. anatina* was also higher in May then decreasing markedly in July before regenerating in September. The glycogen content of *U. pictorum* was the lowest of all species in May, decreasing in July before regenerating in September, when it reached the highest glycogen content of all species. The glycogen content of *U. tumidus* was higher in May before decreasing in July and becoming stable in September.

The uninfested bivalves generally had higher glycogen content than infested bivalves in every month, with significant differences detected only in July in *S. woodiana*, *A. anatina* and *U. pictorum* (ANOVA, $F = 3.95$, $p < 0.05$; $F = 32.06$, $p < 0.01$ and $F = 3.07$, $p < 0.05$, respectively) and in September in *U. pictorum* and *U. tumidus* (ANOVA, $F = 12.70$, $p < 0.001$ and $F = 4.29$, $p < 0.05$, respectively) when the infestation intensity was high (Fig. 5a, b, c). Based on the standard condition index, differences were also detected between species in every month. However, similarly to the glycogen content, significant differences between the classes of infestation were detected only in July in *A. anatina* and in September in *U. pictorum* (ANOVA, $F = 23.16$, $p < 0.01$; $F = 7.09$, $p < 0.01$, respectively, data not shown).

Both glycogen content and standard condition index of unionids were negatively correlated with wet mass of attached dreissenids for every month analysed. However, the impact of wet mass of dreissenids on the glycogen content was only significant in July in *A. anatina* (Pearson's correlation, $r = -0.916$; Linear Regression, $R^2 = 0.84$, $p < 0.01$, Fig. 6a) and in September in *U. pictorum* and *U. tumidus* (Pearson's correlation, $r = -0.824$ and $r = -0.611$; Linear Regression, $R^2 = 0.68$, $p < 0.001$ and $R^2 = 0.37$, $p < 0.001$, respectively, Fig. 6b). Significant impact on the standard condition index was detected in July in *A. anatina* (Pearson's correlation, $r = -0.755$; Linear Regression, $R^2 = 0.57$, $p < 0.05$) and in September in *S. woodiana*, *U. pictorum* and *U. tumidus* (Pearson's correlation, $r = -0.348$, $r = -0.556$ and $r = -0.553$; Linear Regression, $R^2 = 0.12$, $p < 0.05$; $R^2 = 0.31$, $p < 0.01$; and $R^2 = 0.31$, $p < 0.01$, respectively, data not shown). In the case of *C. fluminea* no relationship was detected in July (Pearson's correlation, glycogen content: $r = 0.059$ (Fig. 6a); standard condition index: $r = 0.146$ (data not shown)).

Discussion

The number of highly invasive bivalves is gradually increasing in European fresh waters and Lake Balaton is no exception. This situation is probably contributing as a cumulative threatening factor to the decline of native unionid populations. In Lake Balaton, fouling of several hundred *D. polymorpha* per unionid has been observed since its establishment 80 years ago (Sebestyén 1937), but no available information existed regarding its direct impact on the physiological condition of native unionids prior to this study. In addition, in recent decades, three new invasive bivalves were introduced into Lake Balaton. *Dreissena polymorpha and D. rostriformis bugensis* can directly affect the native unionids by fouling, whereas all four invasive bivalve species (*D. polymorpha, D.*

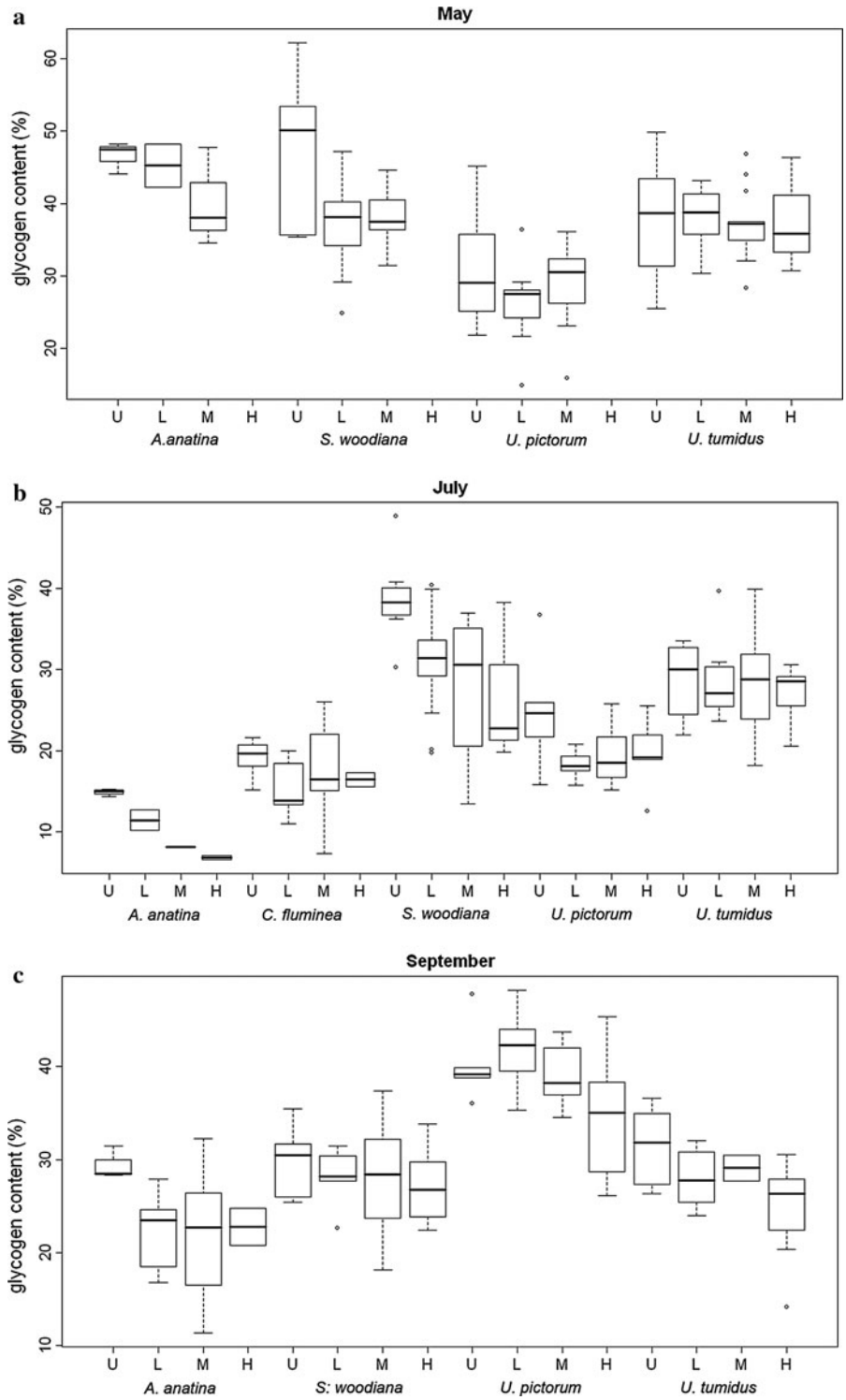

Fig. 5 Glycogen content of the bivalve species studied in May (**a**), July (**b**) and September (**c**) according to infestation intensity: uninfested (U), lightly infested (L), moderately infested (M), and heavily infested (H)

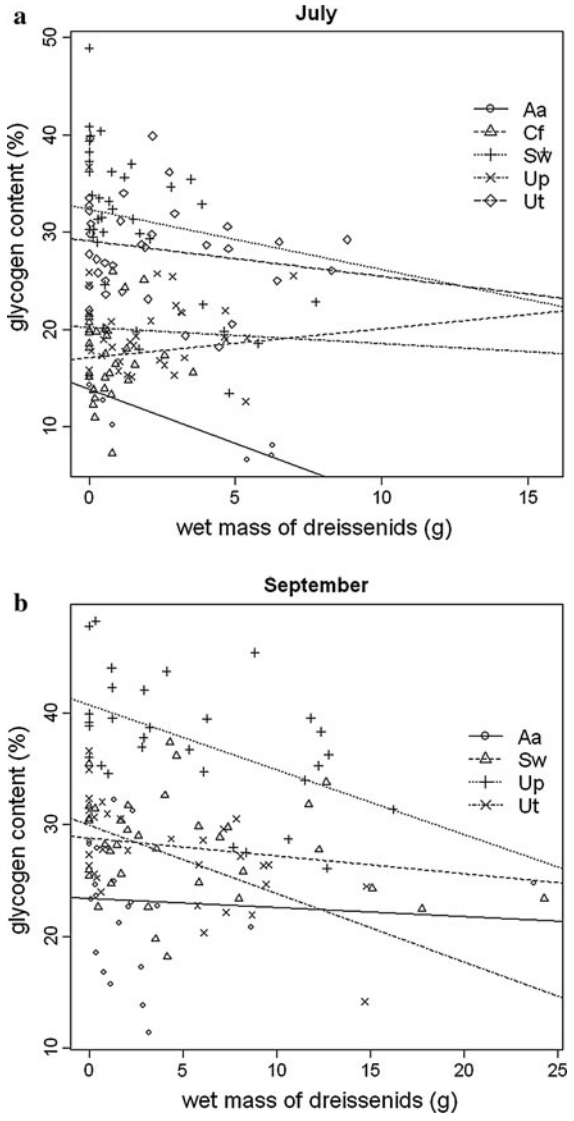

Fig. 6 Linear regressions of the wet mass of attached dreissenids on the glycogen content of the bivalves studied in July (**a**): *Anodonta anatina* (Aa): $y = -1.11x + 13.83$ ($R^2 = 0.84$, $p < 0.01$), *Corbicula fluminea* (Cf): $y = 0.30x + 17.06$, *Sinanodonta woodiana* (Sw): $y = -0.62x + 32.33$, *Unio pictorum* (Up): $y = -0.16x + 20.21$ and *Unio tumidus* (Ut): $y = -0.36x + 29.09$; and September (**b**): *Anodonta anatina* (Aa): $y = -0.08x + 23.37$, *Sinanodonta woodiana* (Sw): $y = -0.16x + 28.83$, *Unio pictorum* (Up): $y = -1.08x + 41.58$ ($R^2 = 0.68$, $p < 0.001$), and *Unio tumidus* (Ut): $y = -0.61x + 29.96$ ($R^2 = 0.37$, $p < 0.001$)

rostriformis bugensis, *C. fluminea* and *S. woodiana*) can also have a significant effect via competition for available resources (food and space, for example; Phelps 1994; Strayer et al. 1999; Sousa et al. 2008a). Furthermore, the co-existence of different invasive bivalves generates an interesting situation in the lake since antagonistic or synergistic effects may occur (i.e. *Dreissena* fouling may directly affect the physiological condition of *S. woodiana* and *C. fluminea*). This situation may interfere with their invasive success or at least change the overall impact of *S. woodiana* and *C. fluminea* (see further discussion below).

All recorded bivalve species inhabiting Lake Balaton were infested by dressenids. The fouling rates for all the unionids increased from May to September, reaching the highest intensity in September, with maximum number and wet mass of dreissenids exceeding 150 specimens/unionid and 20 g/unionid, respectively. In addition, the proportion of heavily infested unionids (>50 specimens) was particularly high in September. One-third of collected *S. woodiana* and half of the sampled *Unio* species were heavily infested by dreissenids in that month. Similar temporal variation in infestation intensity has been observed by Schloesser and Kovalak (1991) in Lake Erie due to the overwinter mortality of dreissenids and their regeneration by larval settlement in summer. In addition, different seasonal burrowing behaviour may also contribute to the temporal variation of infestation, since several studies detected that unionid bivalves burrowed deeper in colder months, whereas many unionids can be found close to the surface in the summer. Therefore, during the summer, unionids may have a larger exposed area, which making them more prone to *Dreissena* infestation (Watters et al. 2001; Schwalb and Pusch 2007; Cyr 2009; Allen and Vaughn 2009). According to our data and a previous study (Sousa et al. 2011a) the major effects are to be found mainly in the summer and early autumn. This phenomenon may be explained by the fact that most of the settled dreissenids cannot survive the harsh winter conditions and thus the level of infestation will be lower at the beginning of spring. Therefore, in order to provide an accurate overall picture concerning the effects of *Dreissena*, future fouling studies should take into account possible temporal variations.

In addition to *D. polymorpha*, we also detected the presence of *D. rostriformis bugensis* attached to unionids albeit in a much smaller quantity (less than 10 %). This situation is in accordance with previous observations predicting that the quagga mussel may also contribute to unionid fouling in the fresh waters of North America, but probably to a considerably lesser

extent than the zebra mussel because it does not show a preference for unionids as substrates (Ricciardi et al. 1995). Nevertheless, between 2009 and 2011 the relative abundance of quagga mussel increased significantly in Lake Balaton and its proliferation will probably continue in the near future since several traits (e.g. higher growth rates, higher filtration capacity, higher ecological tolerance and ability to colonize soft substrate and deeper regions of the lake) make quagga mussel potentially more successful than zebra mussel (Balogh and Purgel 2012). On the other hand, *D. rostriformis bugensis* can rapidly reach large sizes, contributing to a remarkable increase in the overall wet mass of dreissenids fouling unionids. Therefore, if the synergistic fouling effect of dreissenids on the native unionids increases, the risk of extirpation may be higher in the near future.

In line with observations made in a European river (Sousa et al. 2011a), a significant negative impact of *Dreissena* fouling was detected on the physiological condition of native unionids in Lake Balaton in July and September when the fouling intensity was higher. A significant negative impact on the physiological condition of invasive *S. woodiana* was also detected under a high level of infestation. However, we did not find any impact on the physiological condition of the invasive *C. fluminea*, despite the fact that some specimens were heavily fouled (the wet mass of *D. polymorpha* was more than half of *C. fluminea*'s own wet mass). Interestingly, and although the infestation can be expected to be lower on *C. fluminea* since this species spends much of its life cycle buried in the sediments (Britton and Murphy 1977), we found a high number of Asian clams heavily infested, especially taking into account its small size and body mass when compared to the unionid species. Nevertheless, we were not able to find any impact of *Dreissena* on the physiological condition of *C. fluminea* and this situation may be explained by the release of faeces or pseudofaeces by *Dreissena*, which may function as a food resource for Asian clams. Since *Corbicula* has a more variable feeding behaviour (i.e. in addition to filter feeding these clams also have pedal feeding, consuming other sources of organic matter in addition to phytoplankton) it may happen that *Dreissena* subsidies *Corbicula*, increasing (or at least not affecting) their physiological condition (Hakenkamp and Palmer 1999; Sousa et al. 2008a). However, this situation remains speculative and future studies are needed to confirm or reject this facilitation mechanism between these two invasive bivalve species.

Bivalve species showed varying vulnerability to *Dreissena* infestation, which can be explained by their different life history and ecological traits (brooding period, burrowing activity, substrate preference, feeding behaviour, growth rate) and shell morphology (Haag et al. 1993; Burlakova et al. 2000; Raikow and Hamilton 2001; Nichols et al. 2005; Allen and Vaughn 2009; Haag and Rypel 2011; Sousa et al. 2011a). In this study, *A. anatina* and *S. woodiana* had a larger surface area exposed to the water column than *Unio* species, whereby theoretically making *A. anatina* and *S. woodiana* more susceptible to higher levels of *Dreissena* fouling. However, a significant relationship between the greater exposed area and the higher level of infestation was not detected in *A. anatina*. Despite the smaller exposed area, *Unio* species were found to be equally fouled as *A. anatina* and *S. woodiana*. Indeed, dreissenids attached to each other on *Unio* species due to the lack of sufficient surface area. This phenomenon is especially interesting because several studies have demonstrated that *Unio* species are usually buried in the sediment and are rarely overgrown by zebra mussels, while *Anodonta* species are often only partly buried and are colonized more frequently and intensively by zebra mussels (Arter 1989; Aldridge 2010).

The invasive *S. woodiana* had the highest glycogen content of all the unionids studied, which suggests that *S. woodiana* would probably be more resistant to impact than the native bivalve species. Additionally, *S. woodiana* has a typically opportunistic life history strategy (Haag 2012), which may also contribute to a higher resistance. Among native unionids *A. anatina* had the lowest glycogen content and during the presumed brooding period (July) this species had a particularly low glycogen content, which may imply a very high sensitivity to dreissenid fouling. Furthermore, *Anodonta* species typically grow faster and thus presumably have higher energy requirements than *Unio* species, which means that their glycogen level may be more seriously affected by fouling and/or food competition with *Dreissena* species (Haag and Rypel 2011). *Unio tumidus* and *U. pictorum* had a high glycogen content in September following their presumed spawning period. However, despite their large energy reserve, *Unio* species were significantly affected by dreissenid fouling, which may indicate

that these species are also highly vulnerable to *Dreissena* fouling. In summary, our results confirm the potential interspecific differences on the physiological conditions of unionids resulting from *Dreissena* infestation and, more importantly, showed that these effects can be highly variable over time, with the summer and early autumn being the most critical periods.

Interestingly, despite the fact that a drastic decrease in the average density of unionids (Sebestyén 1935; Ponyi 1992) had been observed in Lake Balaton shortly after the establishment of *D. polymorpha*, the native unionid populations escaped extirpation, leading to a co-existence between zebra mussels and native unionids. According to some studies (Ricciardi et al. 1995; Ricciardi 2003) severe unionid mortality (>90 %) occurs when *Dreissena* density and mean infestation intensity reach 6,000 dreissenids/m^2 and 100 dreissenids/unionid. Furthermore, those populations that carry a mean mass of *Dreissena* exceeding 40 % of their own fresh mass will decline in size (by at least 50 %), and with mass ratios greater than 1.0 are likely to become partially or completely extirpated. Recent studies have shown that the highest density of *D. polymorpha* in Lake Balaton can reach 220,000 ind. m^{-2} (Balogh et al. 2008), which is more than 30 times higher than the stated threshold. However, in contrast to the observation made by Sebestyén (1937) shortly after the establishment of *D. polymorpha*, in our study the infestation intensity on unionids reached more than 100 dressenids only sporadically (mainly in September) and only some smaller (approximately 50 mm long) *Unio* specimens were fouled by a wet mass of dressenids equal to or greater than their own wet mass. The current lower infestation of unionids in Lake Balaton compared to North American ecosystems can be explained by several factors, but the most important of which is probably the time of the first invasion. In North America, the *Dreissena* invasion is at an early phase, and the transient effects that occur shortly after the invasion of a new ecosystem are usually much more pronounced and spectacular (Burlakova et al. 2000; Strayer and Malcom 2007). In Lake Balaton, the density of the dressenid populations oscillate regularly, mainly due to the varying competition with Ponto-Caspian amphipods, the frequent and intensive water level fluctuations and the altering predator pressure by waterfowl and fish (Balogh et al. 2008). These factors could reduce the long-term impact of dreissenids and thus provided an opportunity for the survival of the native unionids.

Despite the possible high context dependency of the ecological effects of dreissenids on unionids together with the important role of time since invasion in the overall effects, the consequences of the rapid spread and proliferation of the three newly introduced highly invasive bivalves, including the possible synergistic fouling effects of *Dreissena* species, should be taken into account. Although this study clearly shows the negative impact of *Dreissena* on unionids, we were unable to dissociate this effect from other pressures (e.g. eutrophication, tourism and recreational activities, changes in the fish community that serve as a host for unionids, changes in land and water uses) that can contribute to the decline of native unionids. In addition, care should be taken when extrapolating our results to the whole lake owing to the fact that only two sites were studied, where the density of bivalves and infestation by dreissenids was high. However, over the last decades, the density of the native *A. cygnea*, *P. complanata* and *A. anatina* populations has seriously declined in the whole lake (Benko-Kiss et al. 2012). At our study site located in the Keszthely basin, the density of bivalves was previously detected to be several times higher than in any other part of the lake due to the high levels of nutrients and organic material (Ponyi 1992). Although our study site offers advantageous habitat conditions for bivalves, we did not find *P. complanata* and *A. cygnea* and the recorded mean density of *A. anatina* was very low. A decline in *Anodonta* populations has also been reported in other European lakes. For example, a particularly high mortality of *A. cygnea* was detected in Barden Lake (UK) due to the high level of *Dreissena* fouling (Aldridge 2010) and the density of *A. anatina* and *A. cygnea* considerably decreased in response to the spread of *S. woodiana* in Lake Garda and Lake Maggiore (Italy) (Cappelletti et al. 2009; Kamburska et al. 2013). Indeed, the recently introduced *S. woodiana* reached a high mean density in the Keszthely basin where its invasion presumably began. Densities of *S. woodiana* were more than three times higher than the mean density of *A. anatina*, but it was still lower than the mean density of native *Unio* species. The recent spread and proliferation of *S. woodiana* with its large biomass may also become a serious threat for native unionids. Interestingly, due to the negative physiological impact imposed by

Dreissena on *S. woodiana* its rapid proliferation and overall impact may be slowed down by the increasing intensity of *Dreissena* infestation.

Overall, our data may contribute to a better understanding of temporal variation in fouling intensity and the impact of dreissenids on native European unionids and highly invasive bivalves. In addition, this study may increase knowledge concerning the possible synergistic-antagonistic effects of invasive bivalves and provide the first evidence that the invasive *C. fluminea* appears to be less vulnerable to dressenid infestation than *S. woodiana* and native unionid species.

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